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Female Reproductive Seasonality and Male Influxes in Wild Mandrills (*Mandrillus sphinx*)

Short running title: Mandrill Reproductive Seasonality and Male Influxes

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25 Abstract

26 The correlates of variation in the number of males in primate groups form a long-standing question
27 in primatology. We investigated female reproductive seasonality and the numbers of males in groups
28 of wild mandrills (*Mandrillus sphinx*) in a 25 month camera-trap survey with 160 camera locations
29 in Moukalaba-Doudou National Park, Gabon. We used 1,760 videos to analyse group composition,
30 including the presence of females with new-born infants and with sexual swellings, the number of
31 males present in groups, and male spatial positioning in groups. Female reproduction was seasonal,
32 with a peak in the number of new-borns in the mid-rainy season and a peak in the number of females
33 with sexual swellings in the early dry season. The number of males in the group increased in the dry
34 season, with a much greater increase in the number of mature males (seven-fold) than in sub-mature
35 males (two-fold). The peak number of mature males, but not sub-mature males, in the group lagged
36 significantly behind the peak in the number of females with sexual swellings, suggesting that sub-
37 mature males enter groups before mature males and/or that mature males stay in the group longer
38 after the peak of females with sexual swellings. Mature, but not sub-mature, males appeared
39 frequently near females with sexual swellings. In conclusion, we found a clear relationship between
40 the presence of receptive females and the number of males in the group, and evidence that male
41 competitive ability influences male strategies.

43 Keywords

44 Camera-trap; Mating tactic; Moukalaba-Doudou; Number of males; Video analysis

46 Introduction

47 The determinants of the number of males in a primate group form a long-standing question
48 in primatology (Chapman and Rothman 2009; Kappeler 2000; Kappeler and van Schaik 2002). The

number of females in a social group correlates tightly with the number of males (Dunbar 2000; Mitani et al. 1996). Seasonal reproduction results in overlapping fertile periods, increasing the number of males in the group (Ridley 1986), within-group synchrony of female cycles is related to an increase in the number of males in a group, while asynchrony is linked to a decrease in the number of males (Carnes et al. 2011; Nunn 1999). Some species experience seasonal changes in the number of males in a group. A field study of red-tailed monkeys (*Cercopithecus ascanius*) first described a ‘male influx’, where multiple males enter a social group during the mating season and then mostly depart from the group after the mating season (Struhsaker 1977). Since then, researchers have reported this behaviour in several Old World monkeys, mainly in species with a one-male multi-female social organization (blue monkeys (*C. mitis*) (Cords et al. 1986; Henzi and Lawes 1987); patas monkeys (*Erythrocebus patas*) (Harding and Olson 1986; Ohsawa 2003)), but also in multi-male multi-female groups of lesser hill langurs (*Semnopithecus entellus hector*) (Borries 2000). Females of these species are philopatric and more or less seasonal breeders. In Stuhlmann’s blue monkeys (*C. m. stuhlmanni*), the male influx is largely determined by the number of sexually active females (Cords 2000), which suggests males might decide whether and when to join and leave the group depending on their competitive ability, which varies with their age, rank, and physical features.

Mandrills (*Mandrillus sphinx*) inhabit tropical forests in central western Africa and form non-nested, extremely large social groups of 300 to over 800 individuals (Abernethy et al. 2002; Hongo 2014). Female mandrills are constantly gregarious and thought to be philopatric (Abernethy and White 2013; Setchell et al. 2008). Studies of a captive colony at the Centre International de Recherches Médicales de Franceville (CIRMF), Gabon, have demonstrated that they have seasonal reproduction with an annual peak of females with exaggerated sexual swellings during the dry season and a birth peak in the mid-rainy season (Setchell et al. 2002; Setchell and Wickings 2004), although female cycles are no more nor less synchronised than expected from a chance distribution (Setchell

et al. 2011). A wild population at Lopé National Park, Gabon (Abernethy et al. 2002), and a released group at Lékédi Park, Gabon (Brockmeyer et al. 2015), show similar seasonality in the presence of females with sexual swellings, but no study has yet examined birth seasonality in the wild. Most male mandrills become peripheral to the social group after they are about 6 years old, when they begin to develop secondary sexual characteristics (Setchell and Dixson 2002; Setchell et al. 2006). These males are thought to subsequently emigrate from their natal groups to wander independently, as solitary males are often observed in the wild (Abernethy et al. 2002; Hongo 2014). Wild mandrills at Lopé show a seasonal male influx, with numbers of fully-grown, mature males increasing six-fold and numbers of developing sub-mature males increasing two-fold in the dry season (Abernethy et al. 2002). Captive groups at CIRMF also experience an increase in the number of males when females with sexual swellings are available (Setchell 2016).

The mandrill is one of the most sexually dimorphic primates (Leigh et al. 2005; Setchell et al. 2001), and males have a markedly prolonged growth period before attaining adult size (Setchell et al. 2001). Consequently, there are remarkable physical differences and clear dominant/subordinate relationships between mature and sub-mature males (Setchell 2003). Males compete physically with no coalitions, and the rate of injury increases from five years to peak at 11 to 12 years, when they attain full body mass (Setchell et al. 2006). At CIRMF, the dominance rank of males also increases with age: males first win a dominance interaction with a mature male at a mean age of 9.1 years, and some attain the top rank at a mean age of 10.8 years (Setchell et al. 2006). Dominant males aged eight years or more mate-guard females with sexual swellings, following them persistently and preventing other males from gaining access to them (Setchell et al. 2005). Top-ranking males at CIRMF account for 94 % of periovulatory mate-guarding and 69 % of paternity (Setchell et al. 2005). Nevertheless, subordinate males including sub-mature males are proven to mate with females furtively (Setchell et al. 2005).

We examined female reproductive seasonality and variation in group composition across the year in groups of wild mandrills in Moukalaba-Doudou National Park, Gabon. It is very difficult to observe the behaviour of wild mandrills directly because of their large home range and poor visibility in dense forest. We collected data indirectly by a large-scale camera-trap survey over more than 2 years and conducted demographic analyses using a large number of video images obtained from the camera-traps. We addressed four aims:

- 1) To examine female reproductive seasonality, based on the number of females with new-borns and the number of females with sexual swellings. We predicted that a peak of females with new-borns would occur during the mid-rainy season, and a peak of females with sexual swellings would occur during the dry season, in accordance with previous studies (Abernethy et al. 2002; Brockmeyer et al. 2015; Setchell et al. 2002; Setchell and Wickings 2004).
- 2) To examine variation in group composition across the year. We predicted that the numbers of both mature and sub-mature males in the group would increase during the dry season, but that the number of mature males would increase more than that of sub-mature males, in accordance with a previous study at Lopé National Park (Abernethy et al. 2002).
- 3) To test the relationship between peaks in the number of females with sexual swellings, mature males, and sub-mature males. We predicted that the peak in the number of mature males would coincide with that of females with sexual swellings, while the peak of the sub-mature males might be less closely related to that of females with sexual swellings, because mature males should have a competitive advantage over sub-mature males, in accordance with reports from CIRMF (Setchell 2003; Setchell et al. 2006).
- 4) To analyse the spatial positioning of mature and sub-mature males in groups. We predicted that mature males would stay in proximity to females with sexual swellings at a higher frequency than by chance, but this would be not the case for sub-mature males due to their lower

competitive ability, based on findings at CIRMF that top-ranking males and dominant mature males are responsible for most mate-guarding behaviour (Setchell et al. 2005).

Methods

Study Site and Study Population

Our study area encompassed ca. 500 km² in the eastern part of Moukalaba-Doudou National Park, Gabon (Fig. 1a). Our base was located at S2° 19' and E10° 34'. This area comprises various vegetation types, including selectively-logged primary forest, secondary forest, temporarily inundated forest and savannah, and the elevation is 68–723 m above sea level (Nakashima 2015). The annual rainfall during 2002–2013 fluctuated between 1176 and 2043 mm, and the mean monthly maximum and minimum temperature during 2006–2013 were 26.7–34.3 °C and 18.7–25.0 °C, respectively (Projet de Conservation de la Biodiversité en Forêt Tropicale à travers la Coexistence Durable entre l'Homme et l'Animal (PROCOBHA), unpublished data). There is one dry season typically from May to September and one rainy season from October to April, and it rains little from December to February in some years (Takenoshita et al. 2008). In our study period, daily rainfall did not exceed 10 mm from 18 May to 9 October 2012 and from 19 May to 11 October 2013. A previous study in the area obtained three full counts of mandrill groups of 169, 350 and 442 individuals (Hongo 2014).

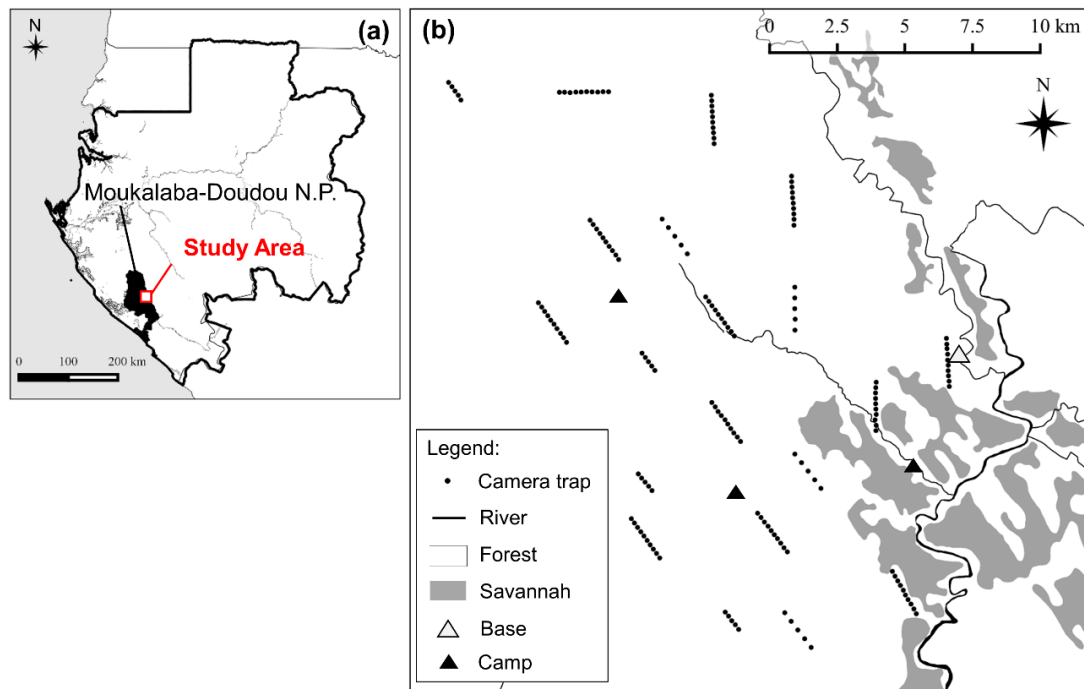


Fig. 1 Study area in Moukalaba-Doudou National Park, Gabon (January 2012–February 2014). (a) Locations of Moukalaba-Doudou National Park, Gabon, and the study area. (b) Locations of camera traps in the study area.

Camera Trapping

We conducted a camera-trap survey for 768 days from 15 January 2012 to 20 February 2014. Prior to the survey, we established 16 line transects of 2 km and four of 1 km in forested areas (Fig. 1b). We deployed five to 10 camera-traps (Bushnell® Trophy Cam 2010, Kansas, US) along each transect at 200 or 400 m intervals. We strapped each camera to a tree 10 m from the line-transect and adjusted it to be parallel to the ground at a height of 30 cm. In total, we deployed cameras at 160 locations. We configured all cameras to start in response to the passage of animals and to record a video image of 30 s or 60 s at a minimum interval of 30 s (3 min from January to July 2012). Longer video recording or shorter interval was impossible because of constraints on the instrument setting

and battery life. We planted two thin stakes in front of each camera to set the ‘counting area’, defined as ‘within 5 m of the cameras’. We visited all transects monthly to monitor the cameras and change batteries if needed.

Video Analysis

We used only images containing mandrills for the current study. We defined a ‘visit’ as consecutive video images taken by the same camera at an interval of less than 30 min (O’Brien et al. 2003). That is, we regarded two videos filmed at a ≥ 30 min interval or taken by different cameras as two independent visits.

Based on information from previous studies of captive mandrills (Dixson 2015; Setchell and Dixson 2002; Setchell et al. 2001, 2002) as well as our own observations at CIRMF and Kyoto City Zoo, we classified recorded animals into age–sex classes as follows:

- ***New-borns*** (0–2 months old): infants with white pelage, clinging to their mothers ventro-ventrally.
- ***Larger infants and juveniles*** (3 months to 3 years old): infants and juveniles distinguishable from new-borns by their olive pelage.
- ***Reproductive females*** (4 years or older): reproductively mature females that we further classified into three categories: *females with new-borns*, *females with (follicular-phase) sexual swellings*, and *females without a new-born and with no (follicular-phase) sexual swelling*. We categorised females with pregnancy swellings, which are clearly distinguishable from follicular-phase swellings (Dixson 2015; Setchell and Wickings 2004), as *females without a new-born and with no sexual swelling*.
- ***Pubescent males*** (4–5 years old): males whose body lengths are similar to those of reproductive females (ca. 50–60 cm) and with small testes.
- ***‘Indistinguishable individuals A’***: animals that we could not distinguish among pubescent males,

- 178 females with sexual swellings, and females without a new-born and with no sexual swelling,
179 because we could not observe their genitals.
- 180 - ***‘Indistinguishable individuals B’***: pubescent males or females without a new-born and with no
181 sexual swelling.
- 182 - ***Sub-mature males*** (6–9 years old): males whose body lengths are larger than those of
183 reproductive females (ca. 60–70 cm), whose testes are larger than those of pubescent males, and
184 whose secondary sexual adornments have begun to develop.
- 185 - ***Mature males*** (10 years or older): fully grown males that have attained a body length estimated
186 to be 70 cm or more.
- 187 - ***Unknowns***: animals that we could not classify.

188 Since we do not know whether the physical characters of wild mandrills develop at the same rate as
189 those of captive animals, and we did not know the ages of the animals, the ages attributed here are
190 approximate guides. Studies at CIRMF (Setchell 2016) use ‘adolescent males’ for sub-mature males,
191 and ‘adult males’ for mature males. We followed Abernethy et al. (2002)’s terms because we estimated
192 ages of animals based on video images of unknown animals, and because we categorized pubescent
193 males as a different class from sub-mature males, both of which are termed adolescent males at
194 CIRMF (Setchell 2003).

195 We defined a ‘group visit’ as a visit that contained two or more individuals and included at
196 least one reproductive female, juvenile, or infant. We used only group visits in analysis. We used only
197 individuals who passed within the counting area for statistical analyses.

198 We recorded sexual interactions (i.e., copulations and genital inspections) and inter-male
199 aggression (i.e., head-bobs, lunges, supplanting, and physical attacks) observed during group visits.
200 We also noted mate-guarding, defined as ‘remaining or walking within 3 m of a female with a sexual
201 swelling’. We also categorized the positional relationships of the mate-guarding pairs as ‘a male

precedes a female with a sexual swelling’, ‘a male follows a female with a sexual swelling’, or
‘position unclear’.

Statistical Analysis

We examined seasonality in group composition and male positioning by constructing generalized linear mixed models (GLMMs) with a binomial error distribution and a logit link function, followed by model selection using Akaike’s Information Criteria (AIC) (Akaike 1974; Burnham and Anderson 2002). We constructed GLMMs using the function ‘glmmML’ in the R-package glmmML (Bronstrom 2013). In each model selection procedure, we selected the model with the smallest AIC value as the ‘best model’ among biologically meaningful candidate model sets, and used models whose AIC differed from the best model (ΔAIC) by less than 2.0 for multi-model inference (Burnham and Anderson 2004). In all statistical tests, we considered $P < 0.05$ as significant. We performed all analyses using R version 3.2.2 (R Core Team 2015).

Reproductive seasonality

We tested the seasonality of the presence of new-borns and of females with sexual swellings using GLMM polynomial regressions. We created data sets by counting the individuals in a group visit. Variables in the full model for the new-born seasonality were as follows: dependent variable = number of females with new-borns/number of all reproductive females; fixed effect = 6th-order polynomial of day of the year (continuous variable of 1–365, 1 = 1st January); random effect = individual visit (random intercept). Similarly, variables in the full model for the seasonality of female sexual swellings were as follows: dependent variable = number of females with sexual swellings/number of all reproductive females; fixed effect = 6th-order polynomial of day of the year; random effect = individual visit.

Variation in the number of males in the group

We tested for variation in the number of mature and sub-mature males in the group across the year using GLMM polynomial regressions. Variables in the full model for the number of mature males in the group were as follows: dependent variable = number of mature males/number of ≥ 4 -year-old individuals except sub-mature males (i.e., mature males, pubescent males, and reproductive females); fixed effect = 6th-order polynomial of day of the year; random effect = individual visit. Variables in the full model for the number of sub-mature males in the group were as follows: dependent variable = number of sub-mature males/number of ≥ 4 -year-old individuals except mature males (i.e., sub-mature males, pubescent males, and reproductive females); fixed effect = 6th-order polynomial of day of the year; random effect = individual visit. We did not include new-borns, larger infants or juveniles in the denominators of the dependent variables above because births may be seasonal and including these classes may make it difficult to obtain a precise estimate of male number.

Additionally, we tested whether the ratio of females with sexual swellings to mature males in each 2-month period (January–February, March–April, etc.) was significantly different from 1.0. To calculate the ratios, we went through the following procedure. First, we counted the number of individuals for each age–sex class by month. Then, we added the numbers of ‘Indistinguishable individuals A’ and ‘Indistinguishable individuals B’ to each class according to the ratio for identified animals (Hongo 2014). That is, we calculated the corrected number of females with sexual swellings (SF^{crt}) in a given month as:

$$SF^{crt} = SF + InA \times \frac{SF}{PM + SF + NF} \quad (1)$$

where SF is the original number of females with sexual swellings, InA is the number of

‘Indistinguishable individuals A’, PM is the number of pubescent males, and NF is the number of females without a new-born and with no sexual swelling. Similarly, we calculated the corrected number of females without a new-born and with no sexual swelling (NF^{crt}) in a given month as:

$$NF^{crt} = NF + InA \times \frac{NF}{PM + SF + NF} + InB \times \frac{NF}{PM + NF} \quad (2)$$

where NF is the original number of females without a new-born and with no sexual swelling, InB is the number of ‘Indistinguishable individuals B’, and the other abbreviations refer to the same classes as in the formula (1). Subsequently, we summed the corrected number of females with sexual swellings and the number of mature males in each 2-month period, and compared them using a two-tailed binomial test. As we conducted this test for the six periods separately, we adjusted P values using Holm’s method (Holm 1979).

Relationships between the timing of peak numbers of females with sexual swellings, mature males and sub-mature males

We tested whether the days when numbers of females with sexual swellings, mature males, and sub-mature males reached a peak were different from each other using a bootstrap method using the difference between two peaks (in days) as a test statistic. We created each bootstrap sample from the original data set and calculated the day of each peak using the best model, then calculated the day difference between the two peaks, obtaining a bootstrapped test statistic value. We repeated this bootstrap resampling procedure 10,000 times to construct a probability distribution of this value, and calculated the probability that the bootstrapped value was equal or larger than the observed one, using this as the P value. As we conducted this test for three pairs (females with sexual swellings vs. mature males, females with sexual swellings vs. sub-mature males, and mature males vs. sub-mature males),

274 we adjusted the P values using Holm's method (Holm 1979).

275

276 *Male spatial positioning and mate-guarding*

277 Prior to the analyses described in this section, we adjusted the time length of all the videos
278 to 30 s by discarding the second half of 60 s videos, to give each video equal weight in our analysis.

279 To test whether males appeared at higher rates in videos including at least one female with
280 a sexual swelling than those without a female with a sexual swelling, we constructed two GLMMs.
281 We created data sets by counting individuals by video image, not by visit. Variables in the full model
282 for the mature male-positioning were as follows: dependent variable = number of mature
283 males/number of all individuals except new-borns and infants clinging to their mothers; fixed effects
284 = presence/absence of a female with a sexual swelling (categorical variable), 3rd-order polynomial
285 of day of the year, and interactions between the above two effects; random effect = individual visits
286 (random intercept). Likewise, variables in a full model for the sub-mature male-positioning were as
287 follows: dependent variable = number of sub-mature males/number of all individuals except new-
288 borns and infants clinging to their mothers; fixed effects = presence/absence of a female with a sexual
289 swelling (categorical variable), 3rd-order polynomial of day of the year, and interactions between the
290 two effects; random effect = individual visits. We did not include the 4th or more order of day as a
291 fixed effect in the full models for male positioning because the calculations failed to converge when
292 we did so.

293 In addition, we extracted videos including at least one female with a sexual swelling and
294 one mature male and/or sub-mature male, and tested whether the proportion of mature males and sub-
295 mature males showing mate-guarding differed using a two-tailed Fisher's exact test.

296

297 Ethical Note

298 This study complied with Code of Best Practices for Field Primatology of the International
299 Primatological Society and the laws of the Gabonese Republic and was conducted with approval from
300 the Centre National de la Recherche Scientifique et Technologique (permission number AR0031/11)
301 and the Agence Nationale des Parcs Nationaux (permission numbers 000017, 000022).

302

303 **Results**

304 The survey period included 64,854 camera-days (daily mean functioning camera = $84.4 \pm$
305 SD 22.8, range: 7–128). We identified 303 mandrill group visits (i.e., 0.47 % of camera-days)
306 containing a total of 1,760 video images and counted 5,906 individuals. A group visit contained a
307 mean of $5.5 \pm$ SD 6.1 video images and a mean of $19.5 \pm$ SD 24.8 mandrills in the counting area. We
308 successfully classified 97.9 % of individuals into an age–sex class (Table 1).

309 **Table 1** Monthly counts of mandrills (*Mandrillus sphinx*) by age–sex class, based on a camera trap survey in Moukalaba-Doudou National Park, Gabon
310 (January 2012–February 2014).

Month	Number of individuals (% of the total number of individuals)											Secondary sex ratio ^b
	New-borns	Larger infant and juveniles	Reproductive females [% of total females]			Total reproductive females	Pubescent males ^a	Sub-mature males	Mature males	Unknown	Total	
			Females with a new-born	Females with a sexual swelling ^a	Females without a new-born and with no sexual swelling ^a							
Jan.	89 (10.4)	310 (36.3)	89 [32.0]	3.6 [1.3]	185.2 [66.7]	277.9 (32.6)	105.1 (12.3)	49 (5.7)	8 (0.9)	14 (1.6)	853	4.9
Feb.	41 (6.1)	275 (40.9)	41 [22.1]	5.8 [3.1]	138.5 [74.8]	185.3 (27.6)	91.7 (13.6)	59 (8.8)	6 (0.9)	14 (2.1)	672	2.9
Mar.	1 (0.5)	75 (39.7)	1 [1.8]	4.0 [7.0]	51.2 [91.2]	56.2 (29.7)	31.8 (16.8)	18 (9.5)	4 (2.1)	3 (1.6)	189	2.6
Apr.	4 (2.3)	80 (45.2)	4 [6.8]	7.7 [13.1]	47.0 [80.1]	58.7 (33.2)	14.3 (8.1)	11 (6.2)	5 (2.8)	4 (2.3)	177	3.7
May	1 (0.2)	184 (44.9)	1 [0.8]	36.4 [29.7]	85.0 [69.5]	122.3 (29.8)	25.7 (6.3)	46 (11.2)	18 (4.4)	13 (3.2)	410	1.9
Jun.	1 (0.4)	82 (29.9)	1 [0.8]	24.3 [20.6]	92.7 [78.5]	118.0 (43.1)	19.0 (6.9)	33 (12.0)	14 (5.1)	7 (2.6)	274	2.5
Jul.	0 (0.0)	135 (36.0)	0 [0.0]	17.5 [13.2]	115.4 [86.8]	132.9 (35.5)	36.1 (9.6)	42 (11.2)	19 (5.1)	10 (2.7)	375	2.2
Aug.	3 (0.8)	147 (37.9)	3 [2.1]	14.9 [10.4]	125.3 [87.5]	143.2 (36.9)	25.8 (6.6)	44 (11.3)	20 (5.2)	5 (1.3)	388	2.2
Sep.	0 (0.0)	204 (37.4)	0 [0.0]	28.4 [14.4]	169.0 [85.6]	197.4 (36.2)	48.6 (8.9)	60 (11.0)	22 (4.0)	13 (2.4)	545	2.4
Oct.	11 (1.2)	390 (44.3)	11 [4.4]	12.4 [5.0]	225.3 [90.6]	248.7 (28.2)	98.3 (11.2)	67 (7.6)	46 (5.2)	20 (2.3)	881	2.2
Nov.	18 (2.9)	319 (50.7)	18 [11.4]	8.2 [5.2]	132.2 [83.5]	158.4 (25.2)	60.6 (9.6)	47 (7.5)	13 (2.1)	13 (2.1)	629	2.6
Dec.	39 (7.6)	232 (45.2)	39 [27.5]	7.1 [5.0]	95.9 [67.5]	142.1 (27.7)	59.9 (11.7)	22 (4.3)	9 (1.8)	9 (1.8)	513	4.6
Total	208 (3.5)	2433 (41.2)	208 [11.3]	178.6 [9.7]	1460.6 [79.1]	1847.2 (31.3)	610.8 (10.3)	498 (8.4)	184 (3.1)	125 (2.1)	5906	–

311 ^a Numbers are corrected for indistinguishable individuals (see Methods); ^b Ratio of the number of reproductive females to the number of mature and sub-
312 mature males

Reproductive Seasonality

The proportion of females with new-borns among all reproductive females varied across the year, with an annual peak in the mid-rainy season, although we observed at least one female with a new-born in all months except July and September (Table 1). Correcting the numbers of females with sexual swellings and females without a new-born and with no sexual swelling for animals that we could not distinguish (see Methods), females with new-borns accounted for 32.0% of reproductive females in January and 27.5% in December. We counted only 10 females with new-borns in total from March to September (1.2% of reproductive females during this period). The best polynomial regression model contained the 2nd-order polynomial of day as a fixed effect, and the second best model showed a similar regression curve to the best model (Fig. 2a; Table 2).

The proportion of females with sexual swellings among all reproductive females showed a peak in the early dry season, although we observed at least one female with a sexual swelling in all months (Table 1). After correcting for animals that we could not distinguish, females with sexual swellings accounted for 29.7% of reproductive females in May and 20.6% in June, while they accounted for only 3.7 % of reproductive females from October to February. The best model contained the 3rd-order polynomial of day as a fixed effect, indicating that the proportion of females with sexual swellings decreased more gradually than it increased (Fig. 2b; Table 2). The second best model showed a regression curve similar to that of the best model. According to the best model, the peak in the proportion of females with sexual swellings occurred on the 156th day of the year (5 June).

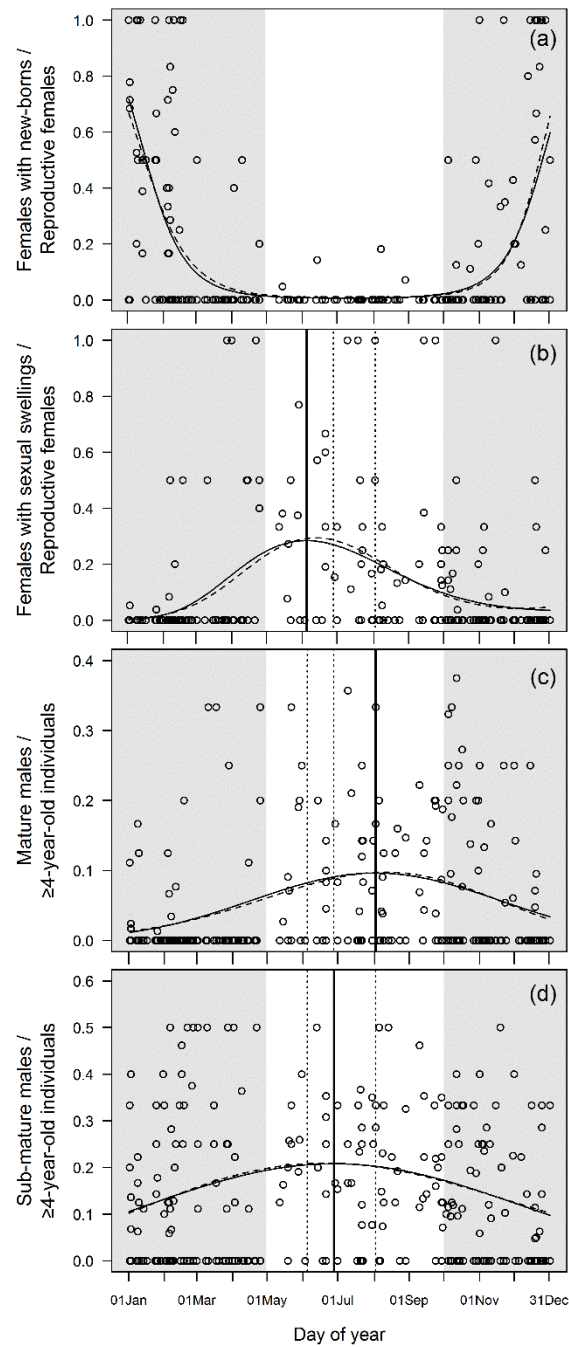


Fig. 2 Variation in the proportions of (a) females with new-borns, (b) females with sexual swellings, (c) mature males, and (d) sub-mature males mandrills in social groups at Moukalaba-Doudou National Park, Gabon (January 2012–February 2014). Data points represent individual group visits. Regression curves of the best (solid) and the second best model (dashed) are shown. Vertical lines represent peak days of females with sexual swellings, sub-mature males, and mature males from left to right. Typical dry season (white area) and rainy season (shaded area) are indicated

339 **Table 2** Parameter estimates, AIC, and Δ AIC values for models of female reproductive seasonality and numbers of mature and sub-mature male mandrills in
340 social groups at Moukalaba-Doudou National Park, Gabon (January 2012–February 2014). Models with Δ AIC <2.0 are shown.

Order	AIC (ΔAIC)	Parameter estimate / SE					
		Intercept	Day	Day^2	Day^3	Day^4	Random effect
Number of females with new-borns among all reproductive females (N = 238)							
1	257.9 (0.0)	1.1 / 0.33	-0.065 / -0.0071	1.7×10 ⁻⁴ / 1.9×10 ⁻⁵	–	–	1.2 / 0.23
2	259.0 (1.1)	0.80 / 0.43	-0.053 / 0.015	8.8×10 ⁻⁵ / 9.2×10 ⁻⁵	1.5×10 ⁻⁷ / 1.6×10 ⁻⁷	–	1.2 / 0.23
Number of females with sexual swellings among all reproductive females (N = 238)							
1	218.1 (0.0)	-6.0 / 0.80	0.076 / 0.016	-3.5×10 ⁻⁴ / 9.3×10 ⁻⁵	4.3×10 ⁻⁷ / 1.6×10 ⁻⁷	–	0.63 / 0.19
2	219.4 (1.3)	-5.4 / 1.0	0.050 / 0.034	-6.5×10 ⁻⁵ / 3.4×10 ⁻⁴	-6.8×10 ⁻⁷ / 1.3×10 ⁻⁶	1.5×10 ⁻⁹ / 1.7×10 ⁻⁹	0.64 / 0.19
Number of mature males among ≥4-year-old individuals except sub-mature males (N = 286)							
1	282.2 (0.0)	-4.5 / 0.35	0.021 / 0.0040	-4.9×10 ⁻⁵ / 1.0×10 ⁻⁵	–	–	0.64 / 0.13
2	284.0 (1.8)	-4.3 / 0.45)	0.016 / 0.010	-2.0×10 ⁻⁵ / 6.5×10 ⁻⁵	-5.2×10 ⁻⁸ / 1.1×10 ⁻⁷	–	0.64 / 0.13
Number of mature males among ≥4-year-old individuals except mature males (N = 290)							
1	385.7 (0.0)	-2.1 / 0.16	0.0091 / 0.0022	-2.5×10 ⁻⁵ / 6.1×10 ⁻⁶	–	–	0.39 / 0.090
2	387.6 (1.9)	-2.2 / 0.21	0.011 / 0.0057	-3.6×10 ⁻⁵ / 3.7×10 ⁻⁵	1.9×10 ⁻⁸ / 6.6×10 ⁻⁸	–	0.39 / 0.090

341

Variation in the Number of Males in the Group

The proportion of mature males in groups varied across the year, with a peak during the late dry season (Fig. 2c). The best model contained the 2nd-order polynomial of day as a fixed effect, and the second best model showed a similar regression curve to the best model (Table 2). According to the best model, the proportion of mature males was lowest in January (e.g., 1.4% of ≥ 4 -year-old individuals on 10 January), and increased to 8.3% on the day when the number of females with sexual swellings peaked. Thereafter, the proportion continued to increase gradually to a peak on the 215th day (3 August, 9.6%), about a seven-fold increase from January, and subsequently decreased. We observed mature males in the group during all months of the year (Table 1). From December to February, 16.5% (19/115) of group visits included at least one mature male, and the percentage increased to 36.7 % (11/30) when considering only visits including 20 or more individuals. Based on these results, a group size of 350 including 160 pubescent males and reproductive females (as recorded at Moukalaba-Doudou, Hongo 2014) should include 2–3 mature males in January, with the number increasing to 14–15 around the day of peak numbers of females with sexual swellings and about 17 around the day of peak numbers of mature males.

The proportion of sub-mature males also varied across the year, with a peak in the early dry season (Fig. 2d). The best model contained the 2nd-order polynomial of day as a fixed effect, and the regression curve of the second best model showed a similar pattern (Table 2). According to the best model, the proportion of sub-mature males was lowest in December (e.g., 10.8% of ≥ 4 -year-old individuals on 20 December), increased two-fold to a peak on the 179th day (28 June, 20.8%), then started to decline. Based on these results, a group of 350 including 160 pubescent males and reproductive females should contain 19–20 sub-mature males in December, with the number increasing to about 42 on the day of peak numbers of sub-mature males.

The ratio of the corrected number of females with sexual swellings to mature males was

significantly larger than 1.0 only in May–June (Table 3), the period of the peak in the numbers of females with sexual swellings and sub-mature males. The ratios in the other 2-month periods were not statistically different from 1.0 (Table 3).

Table 3 Numbers of females with sexual swellings and mature males in mandrill social groups, based on a camera trap survey in Moukalaba-Doudou National Park, Gabon (January 2012–February 2014), and P values from binomial test with Holm’s adjustment.

2-month period	Number of females with sexual swellings	Number of mature males	P value
January–February	9	14	0.40 ^a
March–April	12	9	0.66 ^a
May–June	61	32	0.02
July–August	32	39	0.48 ^a
September–October	41	68	0.062
November–December	15	22	0.32 ^a

^a P values are not adjusted because they are larger than 0.05

Relationships between the Timing of Peak Numbers of Females with Sexual Swellings, Mature Males and Sub-mature Males

The peak in the number of mature males lagged significantly behind both the peak in the number of females with sexual swellings (bootstrap test with Holm’s adjustment: N = 10,000, observed time lag = 59 days, P = 0.013) and the peak in the number of sub-mature males (N = 10,000, lag = 36 days, P = 0.026). The lag in the peak in the number of sub-mature males to the peak in the number of females with sexual swelling was not statistically significant (N = 10,000, lag = 23 days,

P = 0.13).

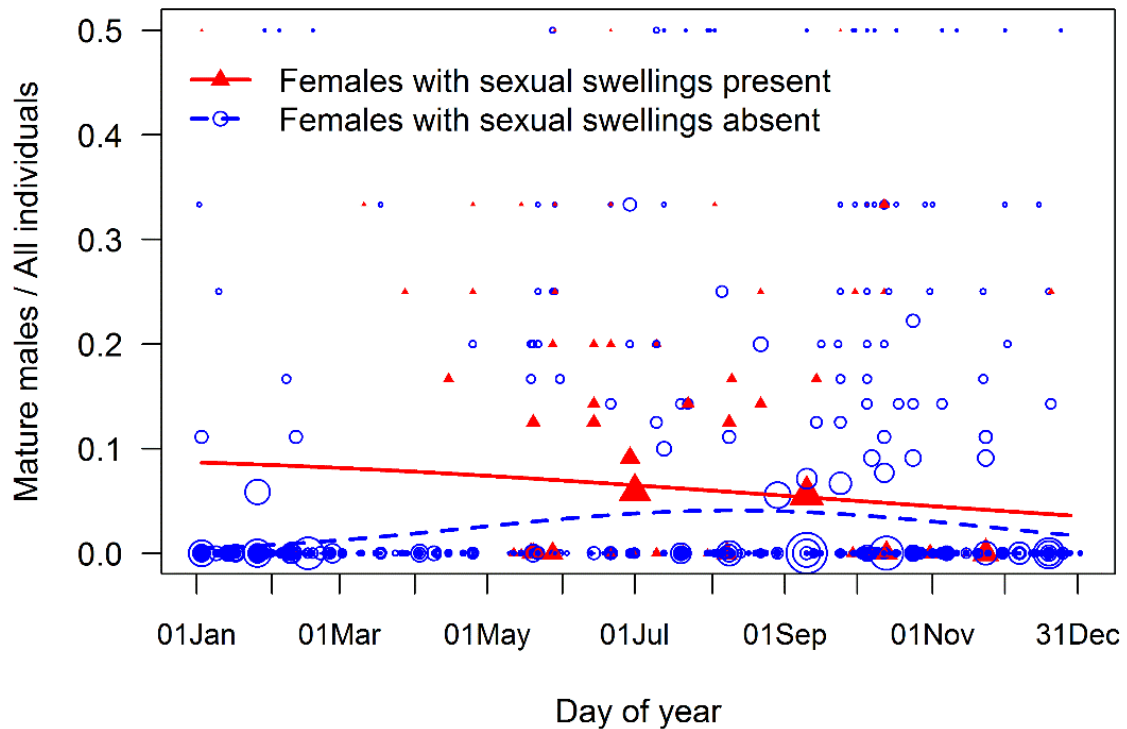
Male Spatial Positioning and Mate-guarding

Overall, 21.0% (37/176) of mature males occurred in videos containing at least one female with a sexual swelling. The best model included the 2nd-order polynomial of day and the presence of females with sexual swellings (Table 4), indicating that the presence of females with sexual swellings positively affected the proportion of mature males, even after the seasonal effect was considered (Fig. 3). In addition, the best model (but not the second best model) also included the interaction term (Table 4), indicating that the proportion of mature males was continuously high in the vicinity of females with sexual swellings even during the birth season although the proportion of mature males in videos without a female with a sexual swelling fluctuated seasonally (Fig. 3). In contrast, the presence of females with sexual swellings had no effect on the proportion of sub-mature males. Only 10.9% (49/451) of sub-mature males occurred in videos containing females with sexual swellings, and the best model contained only the 2nd-order polynomial of day as a fixed effect (Table 4). Although the third best model included the presence of females with sexual swellings, the estimated parameter was negative.

Among males recorded with one or more females with sexual swellings in the same video, more than half of mature males (19/37, 51.4%) showed mate-guarding, whereas a significantly lower proportion of sub-mature males (7/49, 14.3%) did so (Fisher's exact test: odds ratio = 6.18, $P < 0.001$). Of the 19 mature males mate-guarding, 11 followed females with sexual swellings, none preceded females with sexual swellings, and 8 of the relative positions were unclear. We also observed copulation by mature males three times and by sub-mature males twice, and genital inspection of females with sexual swellings once by a mature male and twice by sub-mature males. We observed inter-male aggression six times, three of which were between a mature male and a sub-mature male.

406 Mature males were dominant to sub-mature males in all three cases.

407



408

409 **Fig. 3** Effect of the presence of a female with a sexual swelling and day of year on the spatial
 410 positioning of mature male mandrills in social groups at Moukalaba-Doudou National Park, Gabon
 411 (January 2012–February 2014). Data points show individual video images, and the size of data points
 412 is proportional to number of individuals counted, which reflects the relative importance in regression.
 413 Lines show regression curves of the best model

414 **Table 4** Parameter estimates, AIC, and Δ AIC values for models of spatial positioning in mature males and sub-mature male mandrills in social groups at
415 Moukalaba-Doudou National Park, Gabon (January 2012–February 2014). Models with Δ AIC <2.0 are shown.

Order	AIC (ΔAIC)	Parameter estimate / SE							
		Intercept	Day	Day^2	Day^3	Females with sexual swellings present	Day : Females with sexual swellings present ^a	Day^2 : Females with sexual swellings present ^a	Random effect
Number of mature males among all individuals except new-borns and infants clinging to their mothers (N = 1,627)									
1	761.9 (0.0)	-5.4 / 0.38	0.020 / 0.0044	-4.6×10 ⁻⁵ / 1.1×10 ⁻⁵	–	3.1 / 1.0	-0.021 / 0.011	4.1×10 ⁻⁵ / 2.8×10 ⁻⁵	0.67 / 0.14
2	763.2 (1.3)	-5.2 / 0.36	0.019 / 0.0041	-4.3×10 ⁻⁵ / 1.1×10 ⁻⁵	–	0.67 / 0.22	–	–	0.66 / 0.14
Number of sub-mature males among all individuals except new-borns and infants clinging to their mothers (N = 1,627)									
1	1409.2 (0.0)	-2.8 / 0.17	0.0081 / 0.0023	-2.4×10 ⁻⁵ / 6.3×10 ⁻⁶	–	–	–	–	0.45 / 0.093
2	1410.5 (1.3)	-2.9 / 0.22	0.013 / 0.0058	-5.7×10 ⁻⁵ / 3.8×10 ⁻⁵	6.0×10 ⁻⁸ / 6.9×10 ⁻⁸	–	–	–	0.45 / 0.093
3	1411.2 (1.9)	-2.8 / 0.17	0.0082 / 0.0023	-2.5×10 ⁻⁵ / 6.5×10 ⁻⁶	–	-0.043 / 0.17	–	–	0.45 / 0.093

416 ^a Interaction terms

Discussion

In this study, demographic analyses of video images obtained using camera-traps revealed seasonal patterns of the presence of new-borns and sexual swellings in a wild mandrill population. Our results also showed influxes of both mature and sub-mature males when many females showed sexual swellings and that the numbers of mature males in the group varied more than the number of sub-mature males. Mature and sub-mature males also differed in the timing of the peak numbers and in spatial positioning relative to females with sexual swellings.

Reproductive Seasonality

Our analyses of female reproduction showed seasonality, with a peak in the presence of new-borns in the mid-rainy season and a peak in sexual swellings in the early dry season, generally as predicted (Fig. 2a, b). We observed most new-borns between November and February (Table 1), in accordance with breeding seasonality in captive groups at CIRMF (Setchell et al. 2002). This is the period when fruits are most abundant in the study area (Takenoshita et al. 2008). Since mandrills prefer ripe fruits (Hoshino 1985; Rogers et al. 1996), this may be a female reproductive strategy to give birth and begin lactation during the best period for nutritional intake, in common with many other tropical and sub-tropical primates in Africa and South America (Butynski 1988; Di Bitetti and Janson 2000; Janson and Verdolin 2005; Nakagawa 2000). The proportion of females with new-borns in January (32.0 % of reproductive females, Table 1), suggests that females in the study population may give birth on average once every three years. This estimated interbirth interval is much longer than that observed at CIRMF (405 days, Setchell et al. 2002), and similar to that assumed at Lopé (around two years, Abernethy and White 2013).

Most females showing sexual swellings appeared between April and September (Table 1), as found for captive groups at CIRMF (Setchell and Wickings 2004) and a wild population at Lopé

(Abernethy et al. 2002). Birth seasonality was more distinct than seasonality of sexual swellings, suggesting that the seasonal pattern of conceptive cycles is tighter than that of sexual swellings (female mandrills may take several swelling cycles to conceive, Setchell and Wickings 2004). Nevertheless, we observed both females with sexual swellings and females with new-borns in almost all months (Table 1), as reported at CIRMF (Setchell et al. 2002; Setchell and Wickings 2004). This suggests that reproduction is not confined to particular months. Females may cycle outside the usual mating season if they lose their infant (Setchell et al. 2002) and are in appropriate physical condition to conceive and nurse an infant. Moreover, the proportion of females with sexual swellings decreased more slowly than it increased (Fig. 2b), probably due to multiple cycles in females (Setchell and Wickings 2004).

Variation in the Number of Males in the Group

The proportion of both mature and sub-mature males increased during the dry season, although the increase was much greater in mature males (seven-fold) than in sub-mature males (two-fold) (Fig. 2c, d), in line with findings for mandrills at Lopé (Abernethy et al. 2002). This age difference may be at least partially due to the year-round group membership of younger, natal sub-mature males which have not yet dispersed (Setchell et al. 2006). In addition, the two age classes may differ in ranging behaviour when they are not in the group. In Japanese macaques (*Macaca fuscata*), younger non-group males sometimes associate with group members during the non-mating season, while fully-grown non-group males tend to remain solitary during this period (Kawazoe 2015). Solitary sub-mature, but not mature, male mandrills may also sometimes visit groups outside the mating season, resulting in the observation of sub-mature males in groups in other months.

In contrast to mature and sub-mature males, the proportion of pubescent males decreased during the mating season (Table 1). This decrease is not relative to the increase in number of mature

and sub-mature males, since the ratio of pubescent males to reproductive females, which stay in groups year-round and whose numbers should be stable, was apparently lower during the mating season (0.16–0.27 in April to September, Table 1) than during the birth season (0.38–0.49 in November to February, Table 1). Increasing conflicts with older males in the mating season may precipitate emigration of pubescent males from their natal groups (Dixson 2015). However, our results for pubescent males must be regarded as preliminary, because we could not always distinguish between pubescent males and reproductive females, and our camera-traps rarely filmed solitary pubescent males during the study period. At Lopé, males estimated to be aged five years or younger were not found alone and the number of such males in groups did not vary seasonally (Abernethy et al. 2002). We need further detailed investigations before offering any conclusion on this topic.

Relationships between the Timing of Peak Numbers of Females with Sexual Swellings, Mature Males and Sub-mature Males

Contrary to our prediction, the peak in the number of mature males lagged behind that of females with sexual swellings by about two months (Fig. 2). These results may be due to a bias derived from partial records of very large groups by camera-trapping, as age–sex classes show positional differences when mandrill groups cross open areas (Hongo 2014). It is, however, unlikely that these positional differences occurred in the groups filmed in our study for two reasons. First, we installed all camera-traps in forested areas where the animals are less cautious than in open areas. The positional patterns in the group progression are very weak when the animals are less cautious (Hongo 2014) and only juveniles reacted to our camera-traps. Second, our video images included foraging and resting groups, in which the progression patterns should be unclear, as well as moving groups. We therefore suggest that our findings do not result from methodological bias.

The difference between the peaks in the number of mature and sub-mature males may reflect

the differences in their joining or leaving the group, or both. We therefore discuss each of the two potential factors separately. In terms of joining, some, but not all, mature males may have entered groups sometime after the peak in the number of females with sexual swellings, while sub-mature males tended to join groups ahead of the increase in the number of mature males (Fig. 2c, d). This may be due to differences in ranging behaviour when the males are outside groups, as discussed above. Solitary males generally travel shorter distances or for less time than do group males (yellow baboons (*Papio cynocephalus*) Slatkin and Hausfater 1976; mountain gorillas (*Gorilla beringei beringei*) Yamagiwa 1986); therefore, if solitary mandrills range entirely independently during the non-mating season, it may be difficult to find groups and to monitor the reproductive status of females regularly, because groups are highly nomadic (White et al. 2010) and group density is crucially low (White 1994). Non-resident sub-mature males may range not so far from groups and regularly visit groups so as not to miss the peak in the number of females with sexual swellings. The number of females with sexual swellings significantly exceeded that of mature males only in May–June, the period around the peak in numbers of such females (Table 3). This suggests that mature males may be not able to exclude sub-mature males from all mating opportunities at this time, and therefore it may be the most attractive period for sub-mature males to mate with non-guarded females. In contrast, non-resident mature males may be more independent because the energy costs of ranging around groups should be very high due to their exceedingly large body size, and so they may not always find groups in time for the peak in the number of females with sexual swellings, although they may have the competitive advantage over sub-mature males once they enter groups.

In terms of leaving, mature males remain in relatively high proportions for several months after the peak of females with sexual swellings, while numbers of sub-mature males decrease soon after the peak (Fig. 2c, d). This may reflect their competitive ability. Some females show sexual swellings after the peak, so it may be beneficial for relatively dominant mature males to remain in

groups or enter groups after the peak. In contrast, mating opportunities for more subordinate sub-mature males may decrease after the swelling peak because the number of mature males matches that of females with sexual swellings. The limited mating opportunities after the peak in females with sexual swellings may discourage sub-mature males from staying with or entering the group.

Male Spatial Positioning and Mate-guarding

The results of the spatial positioning were as predicted. The presence of females with sexual swellings positively affected the presence of mature males, but had no such effect on numbers of sub-mature males, suggesting that mature males are able to successfully approach females with sexual swellings, while sub-mature males do so only occasionally even when they are in groups (Fig. 3; Table 4). Moreover, mature males mate-guarded females with sexual swellings more often than sub-mature males. Many mature males followed females with sexual swellings, and none was followed by such females, indicating that mature males, not females with sexual swellings, intend to keep spatial proximity. These results suggest that mature males may have a mating advantage over sub-mature males by mate-guarding females with sexual swellings effectively (Setchell et al. 2005), even in extremely large groups. Nevertheless, sub-mature males may also mate occasionally with females with sexual swellings, possibly siring some offspring, as observed in captivity (Setchell et al. 2005).

We observed mature males in groups in all months (Table 1), suggesting that some mature males join and stay in groups even during the birth season. Our result for mature-male spatial positioning suggests that mature males are concentrated near females with sexual swellings during the birth season, when both are scarce (Fig. 3). Because we could not identify these mature males, we cannot conclude whether they visit groups only temporarily (Abernethy et al. 2002) or whether they live in groups throughout the year, as dominant males do under semi-free-ranging conditions and in released animals (Brockmeyer et al. 2015; Setchell and Dixson 2002; Setchell et al. 2006). Our data

do show, however, that some mature males are present in groups even during the birth season, perhaps because they are able to increase their chances of siring offspring by mating with females swelling outside of the mating season. Long-term studies with direct observation are needed to clarify the residence, dominant status and sexual behaviour of these mature males.

Limitations of the study

We classified mature and sub-mature males based on their body length and other morphological traits, such as facial and genital coloration and development of the rump area. However, the development of secondary sexual traits in male mandrills depends on their social relationships, with subordinate mature males having suppressed development, and body lengths also vary (Dixon 2015; Setchell and Dixon 2001; Wickings and Dixon 1992). It is, therefore, possible that we categorised some suppressed mature males as sub-mature males and some well-developed sub-mature males as mature males, potentially affecting our results. Measurement of male secondary sexual adornments will allow us to investigate the influx patterns of subordinate male mandrills, enhancing our understanding of primate alternative reproductive tactics (Setchell 2008; Setchell 2016).

Conclusion and Perspectives

We document variation in the number of mature and sub-mature males in mandrill groups, and differences in their spatial positioning in groups, suggesting that male mating tactics differ depending on their age and social status: subordinate sub-mature males join and leave groups in response to increases and decreases in the number of females with sexual swellings and approach them occasionally; dominant mature males enter groups around the peak in numbers of females with sexual swellings, stay for longer, and mate-guard females with sexual swellings; and some mature males are present in groups, and stay in the vicinity of females with sexual swellings, during the birth

season. Thus, the mating season, out-of-season breeding and differences in male tactics all contribute to variation in the numbers of males in the group.

Our findings suggest adaptive explanations for the highly female-biased sex ratio of mandrill society. The monthly ratio of reproductive females to mature and sub-mature males varied between 1.9 and 4.9 seasonally (Table 1). Sex ratios were more female-biased during the birth season and approached the ratios of the number of reproductive females to the number of reproductive males in other African papionins during the mating season (agile mangabeys (*Cercocebus galeritus agilis*): 2.0 (Devreese et al. 2013); yellow baboons (*Papio cynocephalus*): 2.7 (Altmann et al. 1985); hamadryas baboons (*P. hamadryas*): 2.4 (Zinner et al. 2001); and geladas (*Theropithecus gelada*): 2.0 (Ohsawa 1979)), although the ratios of mandrills are far higher when only fully-grown males are considered. This suggests that the unusually female-biased sex ratio in mandrills derives from sex differences in gregariousness, which are more pronounced during the birth season. Female mandrills form the social core of groups (Bret et al. 2013), and their social relationships are highly matrilineal, with the dominance rank of daughters being immediately below their mothers, as is common in many cercopithecine primates (Dixon 2015; Setchell et al. 2008). Collective movements may be therefore adaptive for female mandrills. In contrast, most male mandrills leave groups when they are unlikely to mate. This may be because a solitary life allows males to avoid intensive male–male competition and injury (Setchell et al. 2006), to use habitats with preferred foods (Hamilton and Tilson 1982) and to reduce their travel distance and time (Slatkin and Hausfater 1976; Yamagiwa 1986). Because of their large bodies, living in groups may be more costly for male mandrills than for females in terms of within-group food competition and long-distance movements. The advantages of individual ranging may allow male mandrills to compensate for energy lost through male–male competition and group ranging, favouring the evolution of their extreme sexual dimorphism in body mass and canine size.

585

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